TRIUNGULIN LARVAE FROM THE WILLIAMS GALAPAGOS EXPEDITION

TRIUNGULINS OF A MELOID BEETLE BORNE BY XYLOCOPA, WITH REMARKS ON THIS TYPE OF LARVA IN THE COLEOPTERA AND STREPSIPTERA.[1]

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(Figures 28–32 incl.).

Among the numerous specimens of the bee *Xylocopa transitoria* Pérez collected by the members of the Williams Expedition to the Galapagos, there is one female from South Seymour Island, taken by William Beebe, which is of particular interest. This specimen bears attached to the posterior part of the thorax a large number of Coleopterous triungulins which undoubtedly belong to some beetle parasitic upon this large bee.

The Xylocopa in question was preserved in a vial of alcohol and after its long voyage to New York and subsequent shipment to Boston still retains most of the triungulins attached to its body (Fig. 28). These now number approximately 100, in addition to some twenty-five which have become detached during transit. With the exception of two on the basal concavity of the abdomen, all are confined to the scutellum and to one side of the posterior declivity of the propodeum where they form a dense yellow mass. Each triungulin rests with the posterior end of its body directed away from the body of the bee. Examination of the individual triungulins shows that they maintain this position by closing the mandibles about a single body-hair of the bee, or by grasping several together in such a way that the branched hairs pass through the space between the closed mandibles and are pressed between these and the interior surface of the head, while the apical portion of the hair passes backward along the ventral surface of the body. Thus attached, the triungulin is further securely anchored by a peculiar modification of the mandibles which are not toothed along the inner

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FIG. 28. *XYLOCOPA TRANSITORIA* Pérez
Attached to the thorax is a group of triungulins of *Horia maculata* Swed.

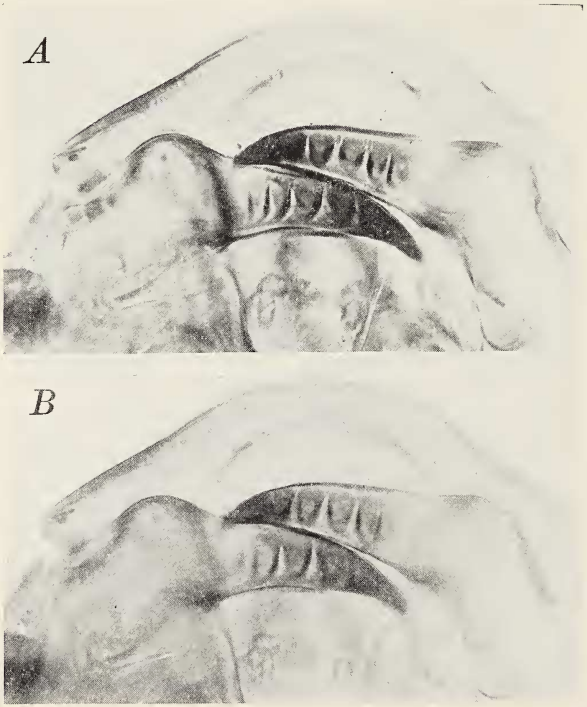

FIG. 29. Mandibles of a triungulin of *HORIA MACULATA* Swed.
In microphotograph –A– the lens has been focussed at a higher level than in –B– to show the narrow spaces between the teeth at their bases.

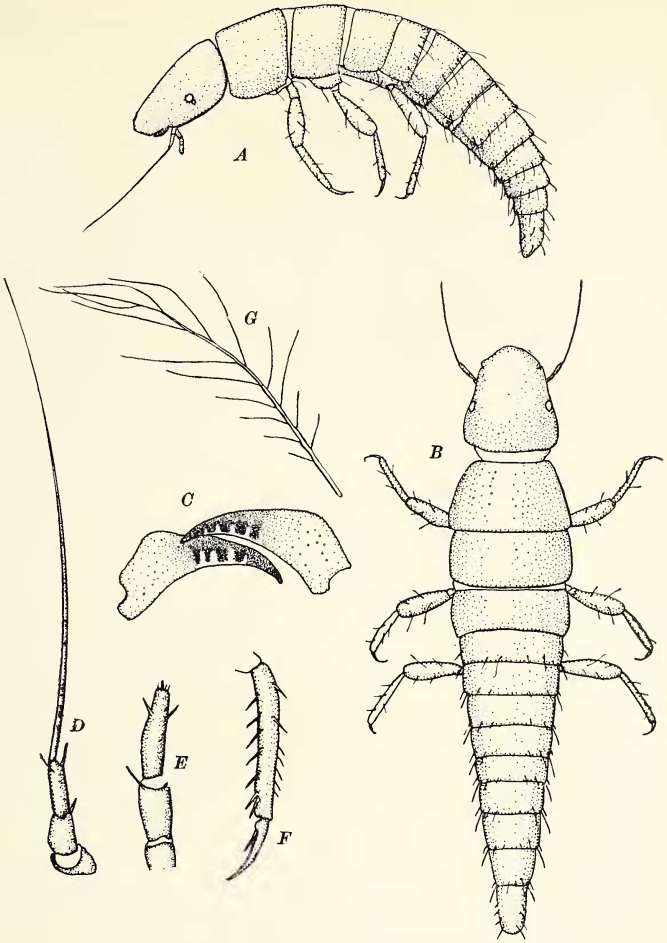

FIG. 30. Triungulin of *HORIA MACULATA* Swed.

A, lateral view; B, dorsal view; C, mandibles; D, antenna; E, palpus; F, tibia and tarsus of hind leg; G, body-hair taken from propodeum of *Xylocopa transitoria* Pérez.

cutting edge as is usual among insects. They are instead provided each with a series of tubercular projections or teeth on the upper surface, that is to say on the side which faces the under surface of the head. Thus when the mandibles are closed (Fig. 30, C; Fig. 29) the projections form a transverse line, each extending backward and serving to catch the hair (Fig. 30, G) so firmly in the notches between them that the triungulin is able to retain its hold continuously in spite of the active movements of its conveyer.

As will appear later, these triungulins are undoubtedly larvae of a species of Horia, most probably *H. maculata* Swed. They may be described as follows:

Length 1.3–1.7 mm. Uniformly pale brownish yellow, the eyes intensely black. Head much flattened; thorax less so, and abdomen nearly cylindrical in cross section. Head gradually narrowed anteriorly, the front border acutely rounded. Eyes set just back of the middle, small, oval, appearing in specimens that have been cleared in potash as composed of two ommatidia, a larger dorsal and a smaller ventral one. Antennae three jointed, very small; basal joint short, second and third cylindrical, the third more slender and slightly the longer; apical seta long and so extremely thin apically that its tip is difficult to see even with an oil-immersion lens; fully as long as the head. Palpi longer than the antennae; basal joint short; second and third longer; tip of third joint truncate and bearing a few very minute setae. Mandibles large, concealed beneath the head when closed; acutely pointed at tip; upper edge (*i. e.*, the surface next to the lower surface of the head) bearing four tooth-like ridges that extend backward. Thoracic segments longer than the abdominal ones; prothorax the longest and the metathorax shortest; all three entirely destitute of bristles. Abdomen long and tapering, composed of nine segments in addition to an apical membranous process (so-called anal sucker; not shown in the figure) which is sometimes extruded to nearly the length of the last segment; all the segments bear along the sides and posterior edge a number of bristly hairs. Legs moderately long, all three pairs of about the same size and form; femora somewhat thickened; tibiae more slender; tarsus (fig. 30, F) reduced to a single curved claw on each leg. The femora and tibiae are sparsely clothed with bristly hairs and each coxa bears one or two bristles.

Having noted the remarkable structure of the mandibles in this species, I was led to examine other triungulins for similar modifications and find that such exist in at least one other form. A female Andrena collected by Prof. W. M. Wheeler at Colebrook, Connecticut, bears attached to the body-hairs, several triungulins quite similar to those on the Xylocopa from the Galapagos, although differing in a number of characters. This larva is probably a Meloid of the tribe Zonitini represented in this region by at least one species, *Zonitis bilineata* Say. According to the studies of Cros ('13; '20) the larvae of this group and of the tribe Sitarini are distinguishable from the triungulins of other Meloidae and of the Rhipiphoridae by the presence of a pair of dorsal projections arising in the membrane between the eighth and ninth abdominal segments, formerly thought to be suckers or attachment organs, but shown by Cros to be respiratory organs. These are present in this triungulin, which further has bi-ocellate eyes and tarsal claws with a long basal bristle. The mandibles are strikingly similar to those of the Horia larvae from

the Galapagos, but are less highly modified. The teeth are on the upper surface of the mandible, but are closer to the edge and actually project over the edge in optical section. This type of dentition is therefore intermediate between that with the usual dentate inner edge and the modification described above where the teeth have shifted away from the edge and have come to lie entirely on the dorsal surface.

Unfortunately no Meloidae or Rhipiphoridae are known from the Galapagos and it is impossible to determine positively the systematic position of the larvae. There are no records which I can find of Xylocopa bearing triungulins in other places where these bees are abundant, but as I hope to show from their structure in conjunction with published records of Meloid beetles reared from the nests of Xylocopa in other parts of the world, the presumptive evidence is very strong that the Galapagos triungulins are those of *Horia maculata* Swed.

In general form, tarsal structure and by the presence of biocellate eyes they are very similar to the larvae of Sitaris, Hornia and other Sitarini and Zonitini as described by Cros ('20), but the respiratory horns near the apex of the abdomen are entirely lacking and they are present in all the members of these tribes in the first larval stage, so far as is definitely known.[2] As mentioned above the form of the mandibles is also different although easily to be derived from a type which occurs in these tribes.

The triungulins of several Meloini are well known and were familiar objects to several of the earlier entomologists. They were observed by Goedart, DeGeer, Kirby and Dufour (who first called them triungulins in 1828), and as early as 1845 Newport was able to explain their presence attached to the bodies of bees on the basis of their larval habits. Later the larva of Meloë was studied by Riley ('77), by Beauregard ('90) and notably by Cros in several recent papers. The legs terminate in three similar curved claws, of equal thickness or sometimes with the median one stouter and straight, two types very aptly termed by Cros "en fourche" and "en trident de Neptune." The head bears a single eye on each side and the abdomen is furnished with long caudal bristles. Obviously the present larva does not belong to this group, although some species

[2] Williams and Hungerford ('14) figure a triungulin which they suspected was that of Hornia, but this is quite likely referable to some other genus of Meloidae.

are bee-parasites and are regularly found attached to the bees. All do not cling to the hairs, however, and one remarkable species, *Meloë cavensis*, actually perforates the intersegmental membrane of the bee by forcing its flat and pointed spiny head between the abdominal plates of its unhappy mount.

Triungulins of a number of genera of the tribe Lyttini are known but none have been found attached to Hymenoptera as they appear to depend entirely upon their own powers of locomotion to locate their hosts. The claws are bifid or tripartite and the eyes are placed far forward, on the anterior half of the head. Our larvae could hardly be referred to this group.

The early larva of the small tribe Horiini is known through a careful study of Bugnion ('09) on the larva of the Ceylonese *Cissites testaceus* and by supplementary details given later by Cros ('20). This larva resembles that of the Zonitini-Sitarini, but lacks the apical abdominal horns, although it is supplied with two caudal setae. The eyes are composed of a single ocellus according to Cros, but there is a suggestion of the eye being double in Bugnion's figure. The leg claws are bifid, consisting of a stout claw with a smaller appendage at the base. In all, the larva is very similar to the Xylocopa-parasite which I have described, and furthermore Cissites inhabits the nests of Xylocopa. Bugnion obtained his material from the galleries of the common Indian *X. tenuiscapa* Westw., with which it has been known to occur since 1833 when Westermann found it in Xylocopa nests where he mistook it for the primary agent excavating the wood. The main differences between Cissites and the form in question from the Galapagos lies in the bi-ocellate eye of the latter, as well as the smaller bristle at the base of the tarsal claw (*cf.* Fig. 31, c.) and in the dention of the mandibles, which are said to be feebly denticulate on the edge in Cissites by Cros, although Bugnion failed to detect any teeth and described them as smooth.

According to Gahan ('08) the genus Cissites is restricted to the Old World, and the Neotropical species which are very closely related are to be placed in Horia. Horia was found associated with Xylocopa nearly a century ago by that well known naturalist and keen observer, the Rev. Landsdown Guilding ('25) on the island of Barbados. He described the later larva of a Horia which he referred to *H. maculata* Swed., but which according to Champion ('92) was undoubtedly that of *H. auriculata* Dugès. Guilding also shows one

of the large brightly marked beetles on the colored plate which accompanies his paper. It is now evident that Guilding was correct in his belief that the Horia is parasitic in the nests of the New World Xylocopas, just as Cissites is in those of Africa and Asia. Champion was not inclined to accept the accuracy of Guilding's conclusions, for he says, in referring to *Horia auriculata* (*loc. cit.* p. 372: "Specimens of this species were chiefly obtained by me in the open verandahs of houses, and on more than one occasion I have observed the insect crawling on the wood-work in the close vicinity of the

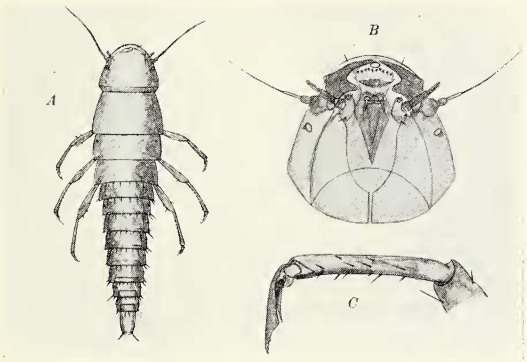

FIG. 31. Triungulin of *CISSITES TESTACEUS* Fabr.
A, dorsal view; B, ventral view of head; C, tibia and tarsus of hind leg. (after Bugnion)

nests of a large blue wasp, these nests being commonly found in such places. It is probable, therefore, that *H. auriculata* really preys upon this wasp, and not upon Xylocopa."

There can be little question that the triungulins which I have described belong to *H. maculata* or possibly to some as yet undescribed species, for *maculata* occurs from Mexico southward to Ecuador, while *auriculata* is not known south of Costa Rica.

One other record of a Meloid associated with Xylocopa has come to my attention. This is an observation by Davidson ('07) and relates to the North American *Nemognatha scutellaris* Lec. which he reared from a cell of Xylocopa, probably *X. orpifex*, as well as from another bee of the genus Alcidamea.

The first stage larvae of the family Rhipiphoridae are not so well known as those of the Meloidae, but those of several genera have been described with considerable care. Like some of the Meloids, Rhipiphorus (*Myodites* auct.) is parasitic on various bees

(Melander & Brues '03; Pierce '04). The triungulin of *R. solidaginis* Pierce has been figured by Silvestri ('06) whose drawing is reproduced in the accompanying figure (Fig. 32, B). It will be seen that this larva is extremely similar in nearly all details to the supposed Horia from Xylocopa described above. Silvestri does not state from whence his specimens came, but as he does not question the identification there is presumably no reason to doubt its accuracy. In his figure of the head three ocelli are shown on one side and two on the other, the larger number being characteristic of Rhipiphoridae

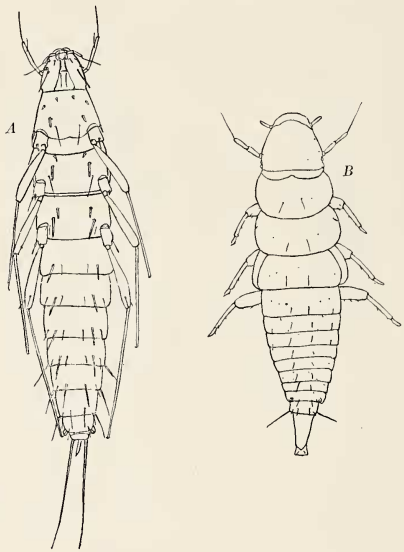

FIG. 32. A, triungulin of *RHYZOSTYLOPS INQUIRENDUS* Silv. Ventral view (after Silvestri)
B, triungulin of *RHIPIPHORUS SOLIDAGINIS* Pierce. Dorsal view (after Silvestri)

and two being characteristic of certain Meloids. The mandibles do not appear to bear any teeth. Pierce's figures ('04) are not sufficiently detailed to show the form of the eyes, nor of the tarsal claws in this species, but he describes the leg as "terminated by a curved claw, almost concealed by a large semi-transparent elliptical pulvillus of twice its length," which is certainly very different from the tarsus in the Meloidae. The first larva of Rhipidius has been several times observed and *R. denisi* Chobaut is well figured by Chobaut ('19). It may be considered together with *Rhyzostylops inquirendus* Silvestri ('06). The latter is a very aberrant Rhipiphorid known

only from the extremely degenerate female and the first-stage larva. Silvestri considered this insect as more or less intermediate between Rhipidius and the Strepsiptera. The triungulins of these two genera are remarkably similar (fig. 32, A, Rhyzostylops). The legs are more slender than those of the Meloidae, with long thin tibia, tipped by a pair of extremely minute claws, the eyes are multi-ocellate and the body is heavily bristled. In at least some species of Rhipidius (Murray '70), there is a large pulvillus between the tarsal claws. The mandibles are simple, without teeth.

In another Rhipiphorid, Macrosiagon (=*Emenadia*) which occurs in the nests of certain solitary wasps (Odynerus, Eumenes, etc.) there is a pulvillus also, much as in Rhipiphorus.

The structure and arrangement of the claws of the legs of Meloid and Rhipiphorid triungulins is of particular interest in connection with the possible relationship of these beetles to the Strepsiptera. The triungulins of the latter are usually destitute of claws on the legs, which are tipped with flattened sucker-like pads. In some Strepsiptera, however, two pairs of legs bear the terminal sucker while the other is provided with a single claw. This is the case in *Xenos nigrescens* Brues as figured in a former paper ('05) and a recent re-examination of these triungulins leaves no doubt as to the actual dissimilarity of the legs, the hind pair each with a claw and the four anterior legs each with a terminal disc. The same arrangement occurs in an undetermined genus "allied to Xenos" figured by Perkins ('05) and in Stylops.

Terminal pads on all three pairs of legs occur also in some Strepsiptera, at least they have been so figured in Stichotrema (Pierce '18). Single claws on all the legs are present in several genera, *e. g.*, Elenchus (Perkins '05), Pentozocera (=*Bruesia* Perk.) (Perkins '05) and in *Stylops californica* Pierce (Pierce '18) although the presence of discs on the four anterior legs of some other species of Stylops would make it seem probable that *S. californica* must represent another genus.

Triple claws on each leg have been found by Pierce ('18) in Callipharixenos which thus approaches the typical Meloid triungulin in tarsal structure, although the claws are very delicate and appear as three slender filaments attached to a distinct elongate tarsal joint.

Thus it will be seen that the Strepsipteran triungulins show a great variation in regard to the terminal armature of the legs and

exhibit no constant character which will serve to distinguish them from those of either the Meloidae or Rhipiphoridae. There appears to be no distinguishing characteristic in the presence of long caudal setae as these while present in all Strepsiptera are as well developed in many Meloids and Rhipiphorids. Whether the difficulty of distinguishing the larvae of the two groups indicates genetic relationship is of course not altogether clear, but the many similarities strengthen the opinion held by many entomologists that the Strepsiptera are more closely related to the Coleoptera than to any other group of insects.

This is one of the series of scientific papers of the Harrison Williams Galapagos Expedition, under the directorship of William Beebe, sent out by the Department of Tropical Research of the New York Zoological Society. The general account and narrative of the expedition, together with the natural history and photographs of the fauna, are embodied in a volume by William Beebe, published by G. P. Putnam's Sons, under the auspices of the Zoological Society. Its title is "Galapagos; World's End."

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